Aquatic Angiosperms in Coastal Saline Lagoons of New South Wales.
II. The Vegetation of Tuggerah Lakes, with Specific Comments on the Growth of *Zostera capricorni* Ascherson

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The distribution and relative abundance of the three aquatic angiosperms in the Tuggerah Lakes system have been mapped. The seagrasses occupy an estimated 19.11km^2 or 25% of the area of the lakes. *Halophila ovalis* occurs over an area of 10.40km^2 and *Ruppia megacarpa* over 8.24km^2. The growth rate of *Zostera capricorni* was measured in the field using a hole-punching technique. Growth rates measured over a year ranged from 0.8mg.shoot^{-1}.day^{-1} in winter to a summer maximum of 2.6mg.shoot^{-1}.day^{-1}. There were marked seasonal changes in the storage and use of starch in the rhizomes, from a maximum at the end of summer (226mg.g^{-1}dwt of rhizome) to a minimum value of 20mg.g^{-1} at the end of winter.

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INTRODUCTION

The aquatic vegetation of Tuggerah Lakes was surveyed by Higginson (1965) and some ecological effects of pollution documented (Higginson, 1971). Since that time there have been a number of detailed surveys of the aquatic vegetation of the lakes but these have not been published in full or in generally available literature. A single value for the area of seagrass beds is given by West *et al.* (1985).

This paper provides a full survey of the distribution of seagrasses in Tuggerah Lakes in summer 1985. In addition data are provided on the seasonal aspects of growth of *Zostera capricorni* Ascherson which is the most abundant marine angiosperm in the lakes. Basic data are provided on seasonal variation in shoot length, shoot weight, reproductive status and rhizome starch reserves. Seasonal change in the rate of growth of the vegetative shoot was estimated by the rate of production of new leaf tissue.

TUGGERAH LAKES

Tuggerah Lakes, approximately 100km north of Sydney on the east Australian coast (Fig. 1) are a series of three interconnected coastal lagoons: Lake Munmorah, 7.8km^2; Lake Budgewoi, 11.2km^2; Tuggerah Lake, 58km^2 (total area 77km^2) (Interdept. Comm., 1979). West *et al.* (1985) measured the water surface area at only 70.29km^2 and this reflects the shallow topography: a small fall in the lake level exposes much of the lake bottom especially on the Budgewoi Flats on the eastern margin of Lake Budgewoi. The lakes extend 16km in a north—south direction and 5km east—west with a perimeter of approximately 110km. The lakes are a barrier estuarine system at a relatively youthful stage (Roy, 1984) and are thought to have been formed by long shore currents building a series of sand bars across an indentation in the coastline. The eastern foreshores are thus of a sand-dune nature (Bird, 1984). The lakes are shallow, the average depth being

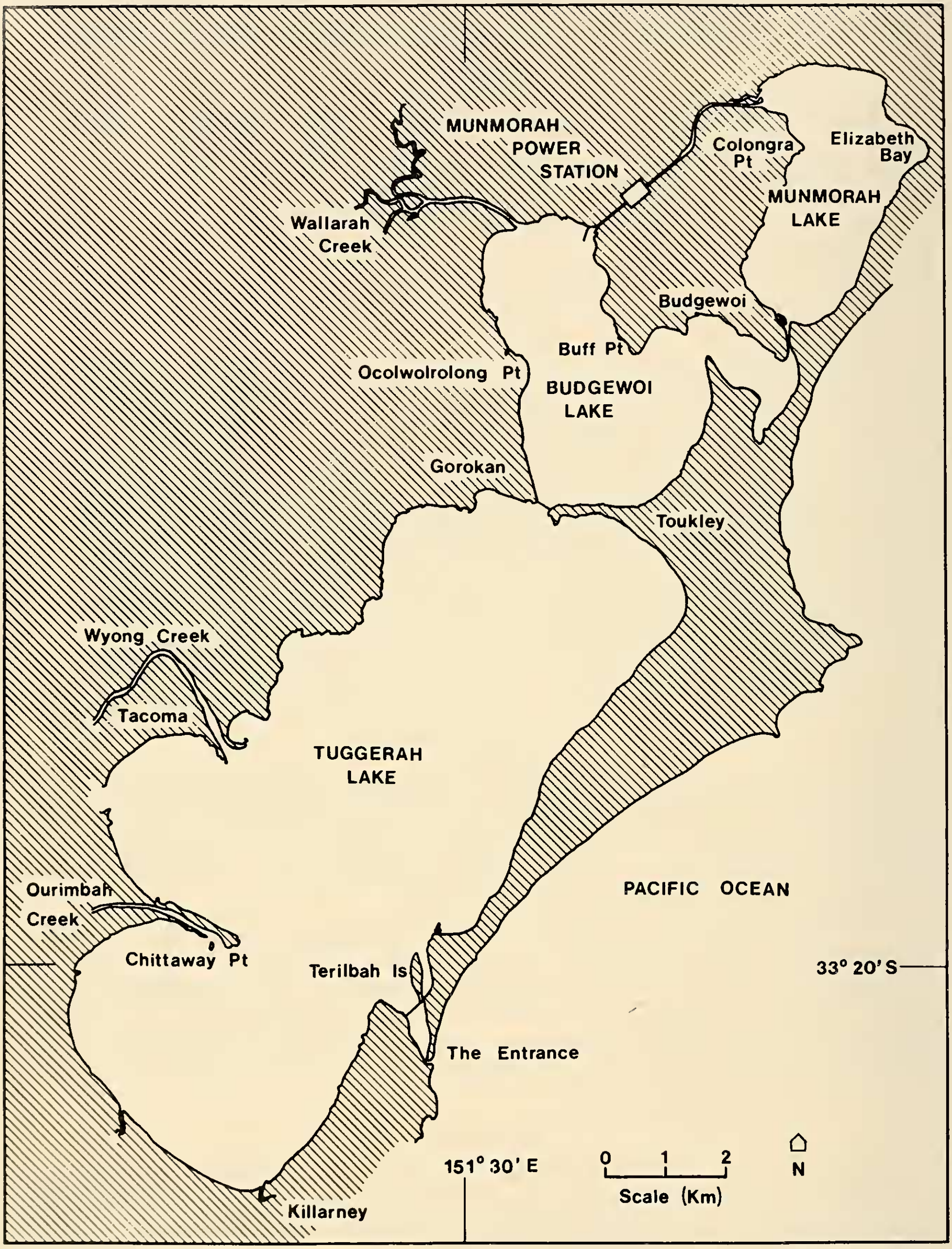

Fig. 1. Tuggerah Lakes showing localities mentioned in the text, and the principal study site for growth studies.

1.9m, and the greatest depth 4.9m under the Toukley bridge between Budgewoi and Tuggerah Lake. The lake system is connected to the sea by a narrow channel at 'The Entrance' and this connection is only rarely completely closed. Tidal flushing is low, with an exchange of only about one per cent of lake volume; tidal action within the lakes is negligible. Salinity is thus dependent on rainfall in the catchment of 670km^2

(Interdept. Comm., 1979). Salinity is generally in the range 17-28 though salinities as low as 5 after heavy rainfall, and 49 after drought, have been recorded (Higginson, 1971).

METHODS

A. *Seagrass distribution survey*

The seagrass distribution was surveyed and mapped using the method outlined in King (1986b), then plotted using the same scale: abundance [1 = sparse growth, (<15% cover); 2 = moderate growth (15-50%); and 3 = abundant growth (>50%)] and sociability [a = individual strands or clumps; b = patches to 10 m; and c = beds of relatively even distribution].

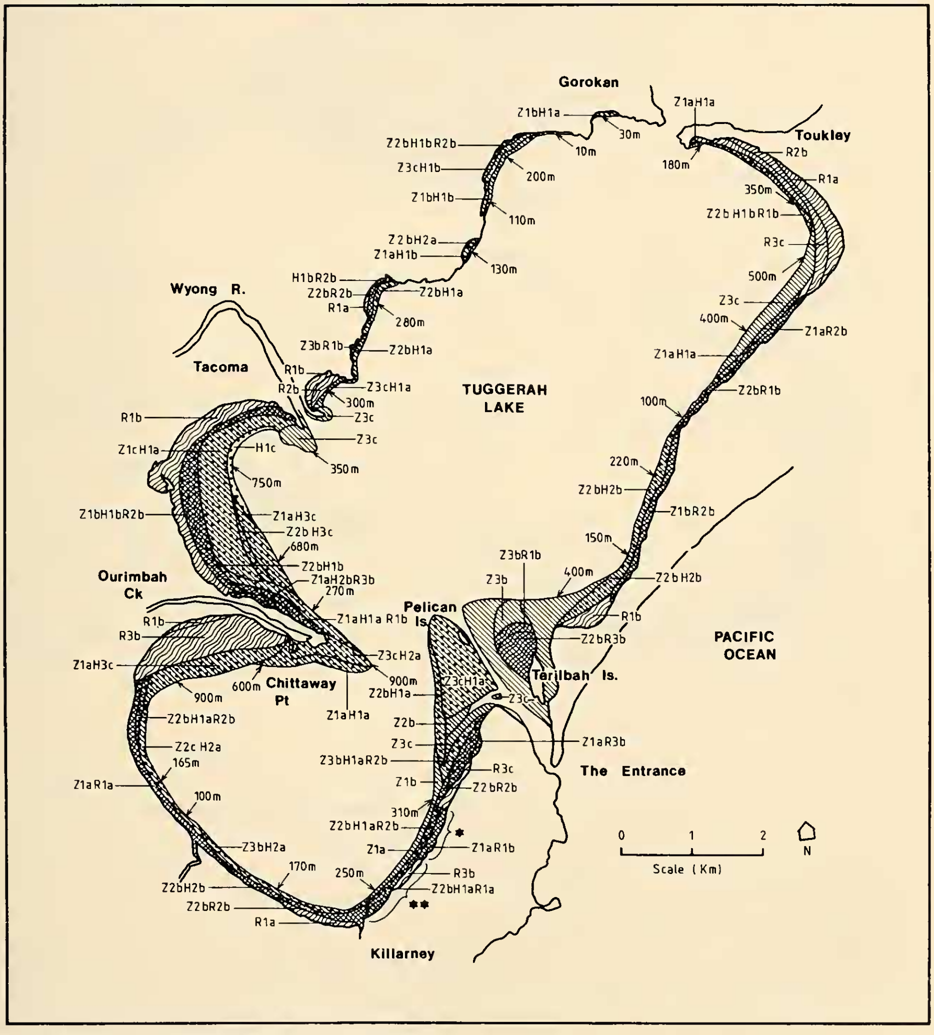

Fig. 2. Distribution of seagrasses in Lake Tuggerah.

▧ *Zostera* ⁙ *Halophila* ▨ *Ruppia*

For key to abundance and sociability see text.

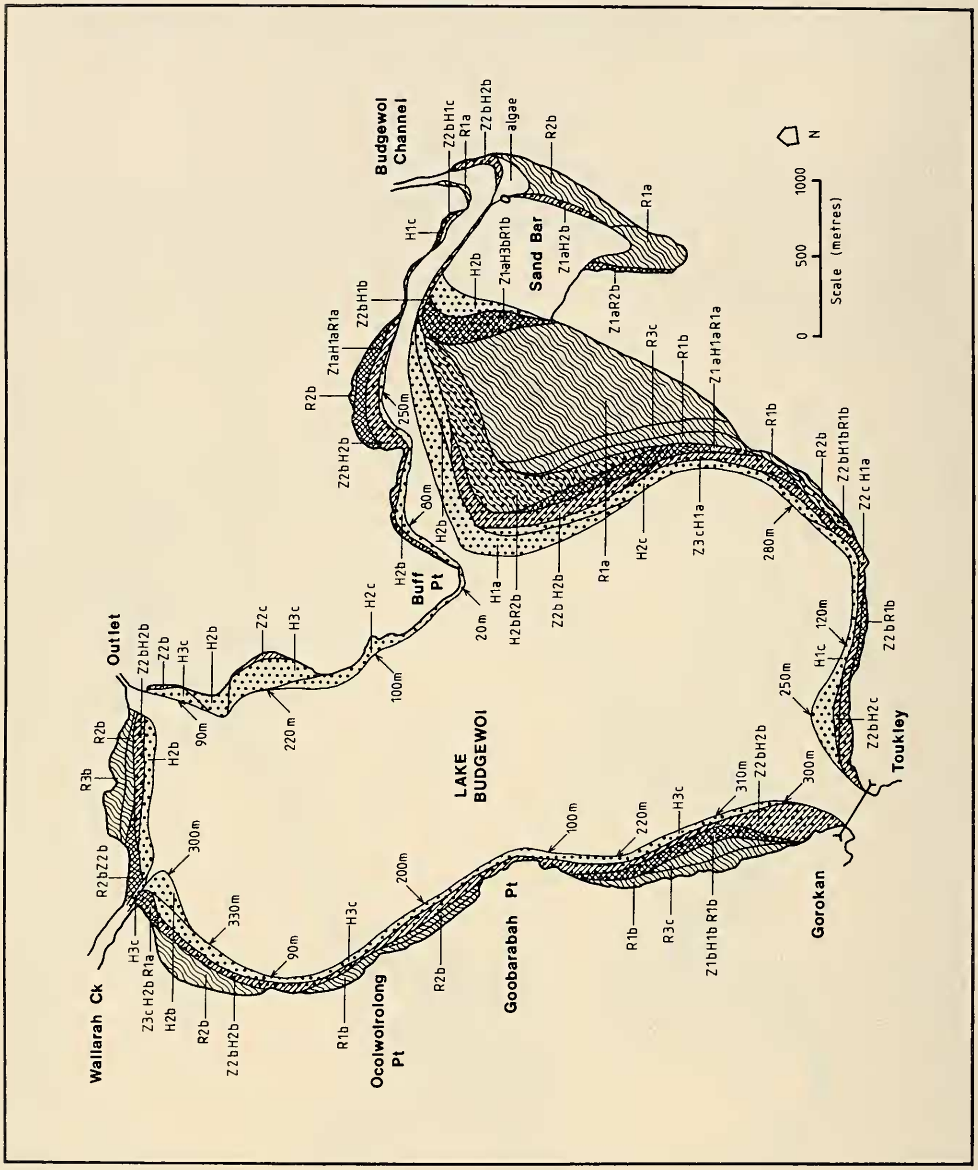

Fig. 3. Distribution of seagrasses in Lake Budgewoi (see legend for Fig. 2).

B. *Seasonal studies on* Zostera capricorni

Study site:

The principal study site for seasonal growth studies was located in a depth of 0.5m in the northwestern end of Lake Munmorah. This site was selected as representative of relatively undisturbed *Zostera* beds. It was well beyond the thermal influence of the Munmorah power station and urban pressure in terms of housing construction, and hence increase in siltation and nutrients, is low. There is little recreational use of these shallow flats. Extensive beds of *Zostera capricorni* up to 500m wide, in some places mixed with *Halophila ovalis*, occurred in this area of the lake (Fig. 4).

1. Leaf growth

Leaf-blade growth rates were estimated using a modification of the leaf-marking technique of Zieman (1974). In these experiments the datum mark in a shoot was a small hole punched through the group of leaves using a pair of 'tongue forceps', the prong of which had been ground to a sharp point. The scissor-like instrument minimizes damage to the leaf blade, which is not crushed. In a preliminary experiment to test the use of this method, holes were punched along the *Zostera* leaves at 2cm intervals, the first hole being about 2mm from the shoot — rhizome junction. The plants were then grown in perspex tanks in a growth cabinet at 25°C for 7 days. Individual leaves on each shoot were then examined to determine possible effects of the marking method, elongation between successive holes, and the relationship between leaf age and elongation rate.

Growth experiments were carried out at 2-month intervals (Oct. 1978 — Feb. 1979) and then at monthly intervals from March 1979 to February 1980. Samples of the *Zostera* were collected from the study site using a 20cm corer, 'planted' in plastic containers, marked and returned to the field. Plants were then harvested after an interval of 12 days and the dry weight (constant weight at 105°C) obtained for new tissue and leaf material above the datum mark. All epiphytes were removed. Growth rates were calculated as increase in biomass per shoot, per day. Each growth experiment was replicated four times.

2. Population data

The following data were obtained in conjunction with the growth experiments:

Shoot length — the length of the longest leaf on each of 50 randomly-selected intact shoots was measured.

Shoot weight — data on shoot weight were obtained directly from the leaf growth study.

Reproductive shoots — only vegetative shoots were used in the calculation of growth rates. The frequency of reproductive shoots was estimated for all core samples.

3. Rhizome starch reserves

Living rhizome segments were collected from September 1978 to February 1980. Each sample consisted of segments from 10-15 plants. The rhizome segments were washed free of sediment, the roots and shoots were removed, and the samples were then frozen and stored at -15°C until extraction. The quantity of starch in the rhizomes was determined using the extraction and assay procedure of Hassid and Neufeld (1964).

RESULTS

A. *Seagrass distribution*

Three aquatic angiosperms occurred in the Tuggerah Lakes in sufficient amounts and widely distributed enough to be mapped at the scale used. These were *Zostera capricorni* Ascherson; *Halophila ovalis* (R. Brown) Hooker f.; and *Ruppia megacarpa* Mason. The maps constructed from the vegetation survey are presented as Figs 2-4. A full copy of the survey is available in King (1986a). The total area occupied by seagrass was 19.11km^2 and the area occupied by each species is presented in Table 1. Data are given separately for each lake in the Tuggerah Lakes system, as well as for the Budgewoi Flats region.

B. *Seasonal studies*

Preliminary growth studies

In the preliminary experiments on material grown in the growth cabinet all leaf elongation occurred within 4cm of the shoot base. Over 90% of growth occurred in the

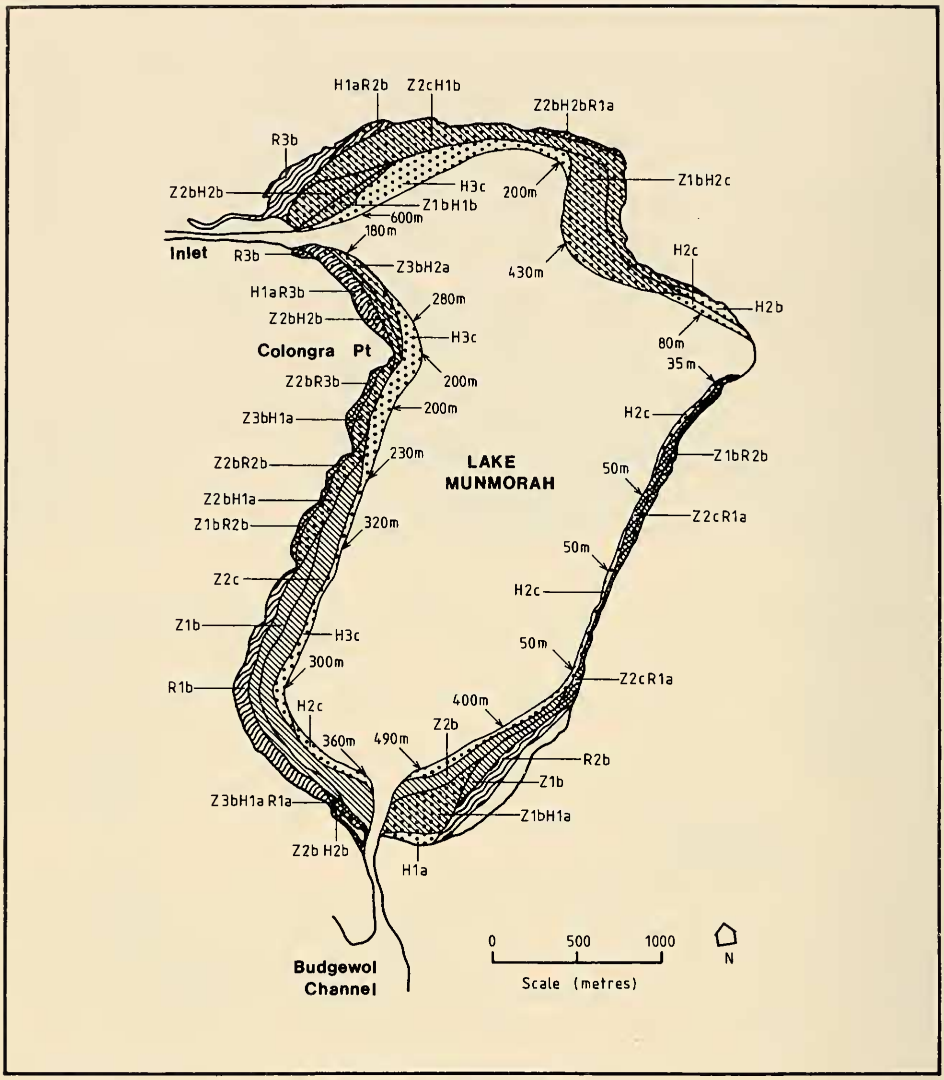

Fig. 4. Distribution of seagrasses in Lake Munmorah (see legend for Fig. 2).

TABLE 1

Areas (km^2) of seagrasses in Tuggerah Lakes, survey of January-February 1985

	Zostera	*Halophila*	*Ruppia*	Total area of seagrass
Tuggerah Lakes (all areas)	12.26	10.40	8.24	19.11
Tuggerah Lake	9.58	6.43	5.48	12.69
Budgewoi Lake	1.19	2.49	2.22	4.03
Budgewoi Flats (within L. Budgewoi)	0.59	1.34	1.71	2.63
Lake Munmorah	1.49	1.48	0.54	2.39

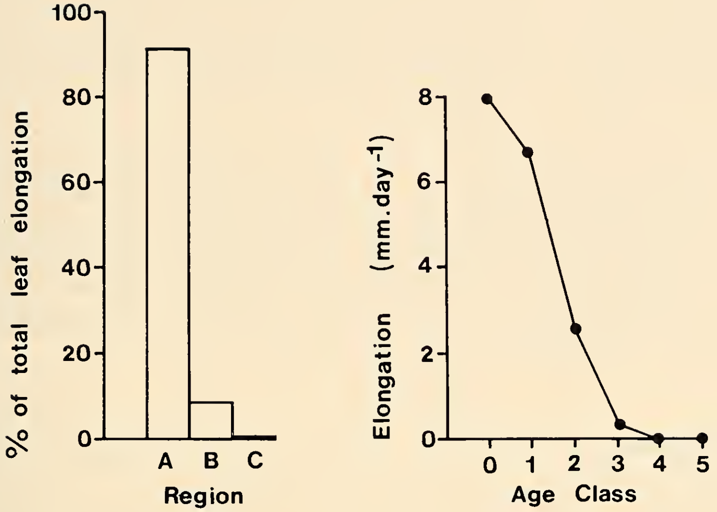

Fig. 5. **a** (left), Elongation between successive holes in *Zostera capricorni*. A represents the growth below the datum (0 cm), B (0-2 cm), C (2-4 cm) and D (above 4 cm). **b** (right), Elongation rates of leaves of different age classes. The youngest marked leaf is referred to age class 1; leaves arising during the course of the experiment as age class '0'.

region below the first hole (at 2mm) and 99.5% below the 2cm datum mark (Fig. 5a). A datum mark 2cm from the base was selected therefore for use in all further experiments. The number of leaves per shoot varied from 3 to 6, and the rate of growth was directly related to leaf age (Fig. 5**b**). Leaves which arose during the harvest interval are indicated as age class '0', and the elongation rate was estimated on the assumption that these new leaves were present on average for half the experimental growth period (Sand-Jensen, 1975).

Leaf growth

The growth rate of new leaf tissue ranged from 2.6 ± 0.5mg. shoot^{-1}.day^{-1} in summer to 0.8mg. shoot^{-1}. day^{-1} in late autumn (Fig. 6). Leaf tissue production was closely related to the weight of the shoot. Shoot viability, (i.e. the percentage of shoots alive at the end of the harvest interval) was generally high (90-100%) except in November and December 1979 when it was 72 and 57% respectively.

Population data

Shoot length

Mean shoot length was at its lowest in late summer, and it ranged from 22.7 ± 0.8 cm in March to a winter maximum of 53.9 ± 1.8cm in July (Fig. 7). Analysis of variance showed that monthly differences were significant ($P < 0.005$) and application of Tukey's test (Zar, 1974) showed that a difference in shoot length of 7.3cm was statistically significant.

Shoot weight

Mean weight of shoots was highest in January 1980 (251 ± 12mg. shoot^{-1} and lowest in May 1979 (89 ± 8mg. shoot^{-1}). The data are plotted in Fig. 8.

Reproductive shoots

Flowering commenced in October 1978, and in 1979 in early August. Seed set occurred soon after flowering and in both years reproductive shoots persisted in the population until December. The density of flowering shoots (shoots.m^{-2}) differed markedly in the two years: in 1978 densities of 188 (Oct) and 113 (Dec) were recorded and for the months Aug-Dec 1979 densities were 24, 63, 90, 35, and 31 respectively.

Rhizome starch reserves

Starch made up to 22.6% of the dry weight of the rhizome of *Zostera capricorni*, and there was a marked seasonal change in the quantity stored (Fig. 9). There was a rapid build up in summer with a maximum value of 226mg.g dwt^{-1} in February 1979 and a decline in autumn to a minimum of 20mg.g dwt^{-1}. The method of starch extraction was accurate but time consuming and therefore replicate samples were analysed in only four months. The variability between replicates in these samples was low (coefficients of variation between 7.1 and 18.2%).

DISCUSSION

A. *Seagrass distribution*

In this survey seagrasses were recorded as covering 19.11km^2 or 25% of the area of Tuggerah Lakes. *Zostera capricorni* was the most widely distributed seagrass occurring over 12.26km^2 or approximately 16% of the lake area. *Halophila ovalis* occurred over 10.40km^2 (14%) and *Ruppia megacarpa* over 8.24km^2 (11%). The only other recent figure is that of West *et al.* (1985) who estimated from aerial photographs that seagrass covered 11.62km^2 of the whole lake system. This considerably lower area may result from the fact that *Halophila* beds were not detected from aerial photographs whereas *Zostera* which forms conspicuous beds was. Also West *et al.* (1985) measured a surface area for the lakes 6.7km^2 less than that in the Interdept. Comm. (1979). If this represents a real difference due to the lowering of the water level in the lakes this reduction would be in the marginal area normally occupied by seagrasses, and particularly the Budgewoi Flats would have been not included.

The areas of seagrass recorded in this survey are considerably lower than those found by Higginson (1965; 1968). The areas of seagrass which he recorded in 1963, 1965 and 1966 were 42%, 31% and 28% of the lake area respectively. Not only has the area occupied by seagrass decreased but also the relative importance of the different species. Higginson's maps, based on a survey in May 1963 (Higginson, 1965), showed Lake Budgewoi almost filled with seagrass (76.2% of lake covered cf. 36% in the present study). The whole central region was occupied by *Ruppia* (42% of the lake area). *Ruppia* was also dominant in deeper water in the southern part of Lake Tuggerah so that approximately one-third of the beds were *Ruppia*-dominated communities. By 1966 there was no *Ruppia* in the lake system (Higginson, 1968). The results presented here show that *Ruppia* had again become established in Tuggerah Lake but it was not found in deeper water; rather in shallow areas inshore of the *Zostera* beds. The places where *Ruppia* was dominant were west of Chittaway Point and just south of Toukley in Tuggerah Lake, and on the Budgewoi Flats. The central portion of each of the three lakes was devoid of seagrasses. Details of long period changes in the vegetation are discussed in King and Hodgson (1986).

B. *Seasonal Studies*

The modification of Zieman's (1974) method of measuring seagrass leaf growth was shown to be an appropriate method.

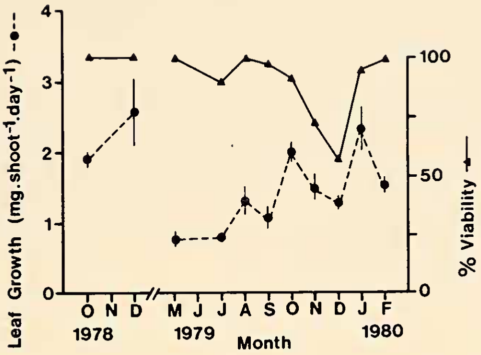

Fig. 6. Seasonal changes in leaf growth recorded on *Zostera capricorni* in the field. Data for early 1979 lost due to vandalism.

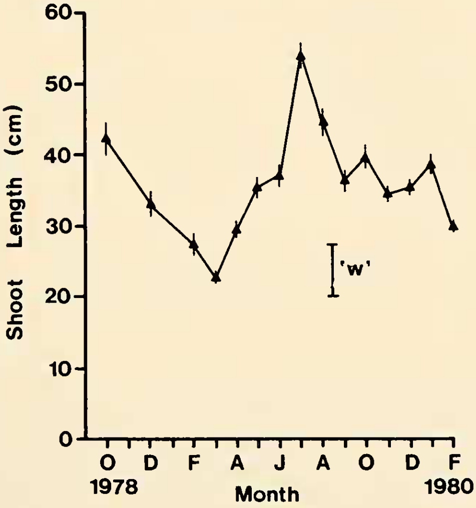

Fig. 7. Seasonal variation in mean shoot length of *Zostera capricorni.* The standard error is shown; the vertical bar (Tukey's 'W') represents a significant difference in shoot length of 7.3 cm.

In the seagrass genera *Thalassia, Posidonia* and *Zostera* the leaf-initiating meristem is at the base of the shoot, just above the rhizome. The meristem is enclosed and protected by the older leaves and leaves are produced distichously from the leaf primordium (den Hartog, 1970). Measurement of leaf growth by marking leaves (Zieman, 1974) assumes that vegetative growth occurs only at the base of the shoot, below a fixed point — the datum mark. Growth involves both the production of new cells and their subsequent expansion, and these two processes are spatially separated. Growth measured as increase in size or weight is mainly due to the process of cell expansion, which occurs in an area adjacent to the meristem (Preston, 1974). In *Zostera* this zone occurs immediately above the meristem and results principally in elongation, since leaf width changes very little during growth (Mukai *et al.*, 1977). This means that leaf growth can be estimated by measuring the single parameter of leaf length, but it is imperative that holes are punched above the zone of cell expansion.

Preliminary experiments indicated that a point 2cm above the shoot—rhizome junction was appropriate as a datum as 99.5% of leaf growth elongation occurred below this point. No deleterious effects due to the hole-punching technique were observed, and all shoots remained healthy over the seven day harvest interval. The holes, though small, were easily located in all leaves. There are advantages in using a punched hole rather than other datum marks such as staples. All leaves can be marked simultaneously, increasing both accuracy and speed. Also the datum mark can be placed below the ligule, through the sheath. In *Zostera* the younger leaves are successively enclosed by the leaf sheaths of older leaves and this restricts alternative types of datum marks to areas above the sheath (Sand-Jensen, 1975). This creates difficulties because of the need to estimate the growth of new unmarked leaves.

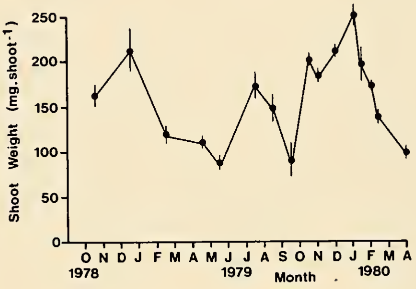

Fig. 8. Seasonal variation in the mean shoot weight of *Zostera capricorni* (± standard error).

In studies of the leaf growth of *Posidonia australis* in altered salinity, Tyerman *et al.* (1984) showed that damage to the leaf sheath killed or inhibited leaf growth. In the present experiments the hole made by the tongue forceps is small and the sheath may reseal. Certainly, there was no visible damage, but it is possible that all new leaf growth was inhibited.

The comparison of growth rates of *Zostera* measured here with those measured in other studies on seagrasses is hampered by the lack of uniformity in the units in which growth rates are expressed, coupled with the fact that the magnitude of the differences is a function of the unit in which growth is measured. In Table 2 data from Botany Bay and Port Hacking are summarized. In so far as generalizations may be drawn from such data one can conclude that the relative differences in growth rates between summer and winter are similar at all these study sites and that even though the measures of relative growth rate are calculated on different bases they are comparable.

The viability of shoots was low during November and December (Fig. 6) and this is reflected in a reduced growth rate during the period.

The range of shoot lengths (22.7cm, late summer—53.9cm in winter) is comparable to that reported by Larkum *et al.* (1984) for *Zostera capricorni* in Botany Bay except that there the pattern is virtually the reverse with a maximum of 45cm in late summer and a minimum of 17.2cm in winter. A similar pattern to that found by Larkum *et al.* (1984) in Botany Bay was reported by Harris *et al.* (1980) for Lake Illawarra, and by Higginson (1968) for Lake Budgewoi. The length of the longest leaves has been used to indicate the seasonal growth cycle (Harris *et al.*, 1980) and the marked seasonal die back which is reported to occur in winter (Wood, 1959b; Larkum *et al.*, 1984). Comparison of the data on maximum shoot length with the leaf growth rates presented above makes it clear that in this case there is no relationship between the two. If *Zostera capricorni* were always to show the marked seasonal fluctuations reported by Wood (1959b) the relationship might be expected but rapid changes in seagrass beds may be caused by factors other than normal seasonal ones, e.g. heavy rainfall (Harris *et al.*, 1980), depredation by swans (Wood, 1959a,b), and wave damage (Kirkman *et al.*, 1982). These factors may be more important in shallow protected lakes such as Lake Munmorah than in open bays, such as Botany Bay. In Lake Illawarra full leaf development has been maintained in some years into early spring, by which time new leaf growth had commenced. Given this it would be better to use the leaf length frequency rather than longest leaf length to establish comparative growth rates (see for example Kirkman *et al.*, 1982).

TABLE 2

Comparative Data for Zostera capricorni *on the New South Wales Coast*

	Summer	Winter
Tuggerah Lakes (present study)		
Measured shoot growth mg. $shoot^{-1}.day^{-1}$	2.6	0.8
Calculated growth rate* g. $g^{-1}.day^{-1}$	0.0104	0.0089
Botany Bay (Larkum *et al.*, 1984)		
Leaf growth cm. day^{-1}	1.62	0.38
'Proportional growth rate' g. $g^{-1}.day^{-1}$	0.0308	0.0213
Production rate g. $m^{-1}.day^{-1}$	8.92	1.37
Calculated shoot growth** mg. $shoot^{-1}.day^{-1}$	4.1	0.8
Port Hacking (Kirkman *et al.*, 1982)		
Production rates g. $m^{-1}.day^{-1}$	2.5	0.3
'Relative growth rate' g. $g^{-1}.day^{-1}$	0.028	0.014

* rate calculated using mean shoot biomass data for Munmorah Lake.
** rate calculated on the basis of mean shoot density.

The data on vegetative shoot weights are not directly comparable with other published data where biomass is generally expressed on the basis of area. Conversion of the data in Larkum *et al.* (1984) gives values ranging from 36mg. $shoot^{-1}$ in winter to 133mg. $shoot^{-1}$ in summer (cf. 89 and 251 in this study). On the basis of average shoot weights the growth rates in the present studies can be expressed in g.$g.^{-1}.day^{-1}$ and thus be compared with the proportional growth rate of Larkum *et al.* (1984). The values obtained are 0.0089 in winter (comparable values for Botany Bay and Port Hacking 0.0213 and 0.008 respectively) and 0.0104 in summer (0.0308 and 0.035). The relative similarity between the rates for summer and winter obtained in this study reflects the less marked seasonal change in above ground biomass compared to that in the other two studies.

Zostera capricorni commences flowering in spring or early summer. Various times for flowering appear in the literature (November — Wood, 1959b; September — Harris *et al.*, 1980; Larkum *et al.*, 1984). In 1978 flowering commenced in October but in 1979 it commenced in early August. The factors initiating flowering have not been investigated but they are possibly related to temperature. In 1979 winter temperatures were relatively mild with the lowest temperature being 13.8°C in July, whereas Electricity Commission data show a minimum generally in the range 11-12°C. Studies on the northern hemisphere *Zostera marina* have implicated temperature in anthesis and seed production (Setchell, 1929; McRoy, 1970; Churchill and Riner, 1978) though Jacobs (1979) suggested that light intensity may be the controlling factor.

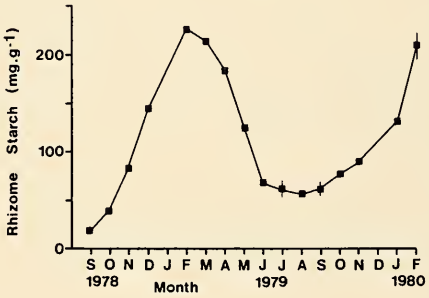

Fig. 9. Seasonal variation in the quantity of starch in the rhizomes of *Zostera capricorni*.

The data on the prevalence of flowering are of the same order as those of Larkum *et al.* (1984) who recorded up to 312 flowers.m^{-2}. The presence of reproductive shoots is apparently not related to the 'success' of *Zostera capricorni* in the Tuggerah Lakes, since establishment from seedlings has not been observed.

The principal storage product in seagrasses is starch, and starch grains are prominent in the cortical cells of rhizomes of *Zostera capricorni* (Fig. 10). Soluble carbohydrates, principally sucrose, are also found in quantity in both the rhizomes and leaves of seagrasses. Drew (1980) reported that *Zostera capricorni* leaves contained 4.7% sucrose, 1.6% myo-inositol and 0.4% fructose while the rhizomes contained 17.1% sucrose.

The extraction method used here (Hassid and Neufeld, 1964) produces a pure starch fraction. This represents stored reserves which need to be enzymatically mobilized before they are available to the plant. Rapid incorporation of starch occurred in summer (approx. 1.5-2.0mg.g^{-1}.day^{-1}) leading to a maximum in early autumn after which the shoot weight began to decline. During autumn and winter the starch level fell rapidly, presumably due to mobilization and use of the reserves by the plant. This fall in the quantity of starch occurred at the same time as the seasonal drop in light intensity and temperature.

Marked seasonal changes in the quantity of both soluble and insoluble carbohydrates are known especially in alpine plants where high levels are essential to initiate rapid growth in the spring growing season (Mooney and Billings, 1960; Bannister and Ward, 1981). The seasonal pattern in aquatic plants differs with low levels of carbohydrates in the rhizomes during winter/spring with rapid incorporation during summer (Haag and Gorham, 1977; Dawes and Lawrence, 1980; Livingston and Patriquin, 1981). The reserves accumulated in summer allow the species to survive low winter light intensities (Dawes and Lawrence, 1980). A comparable situation has been demonstrated in Arctic kelps (Chapman and Lindley, 1980). Defoliation studies with the tropical seagrass *Thalassia testudinum* suggested that rhizome reserves also support leaf-blade regeneration (Dawes and Lawrence, 1979) and Drew (1980) has shown the utilization of endogenous soluble carbohydrates, especially sucrose, by *Zostera angustifolia* leaves starved in the dark.

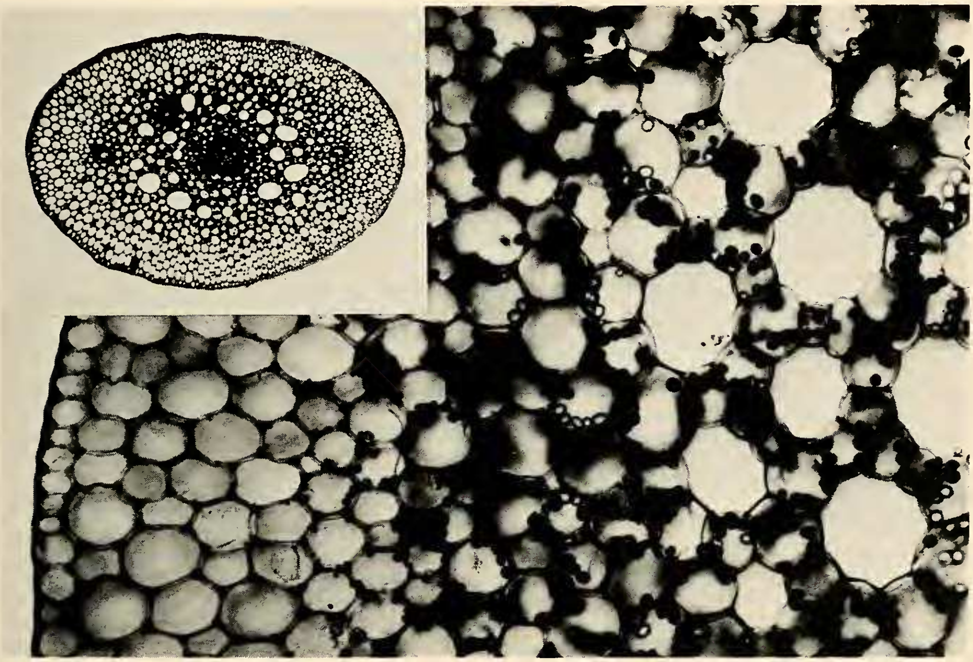

Fig. 10. Transverse section of the rhizome of *Zostera capricorni* showing starch grains in the cortical cells. Material collected late summer, 1985.

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